Reference: *Biol. Bull.* **173:** 461–473. (December, 1987)

QUANTITATIVE GENETICS OF JUVENILE GROWTH AND SHAPE IN THE MUD CRAB *EURYPANOPEUS DEPRESSUS*[1]

THOMAS J. HILBISH AND F. JOHN VERNBERG

Department of Biology and Belle W. Baruch Institute, University of South Carolina, Columbia, South Carolina 29208

ABSTRACT

Rates of growth and development were measured for the first six molts following the crab 1 stage in the mud crab *Eurypanopeus depressus*. The genetic contribution to variation in growth rate, development rate, and shape was determined for each molt interval. Genetic variation in growth rate, measured as increases in both width and length, was evident at most molt intervals. There were also significant genetic effects upon the intermolt interval. Growth rates for each molt interval, calculated on a daily basis to remove the interaction between growth rate and development rate also showed genetic variation. There was no evidence that genetic variation in these parameters changed during early juvenile development; there were substantial levels of genetic variation in growth rate at most ontological stages. Despite high levels of genetic variation for growth rate in dimensions of the carapace, there was no evidence of genetic variation in shape. This analysis does not provide a quantitative estimate of the levels of genetic variance for these traits but does indicate that the magnitude of this source of variance must be very significant.

INTRODUCTION

Variance in many traits may have a large genetic component. High heritabilities have been demonstrated for many traits, including morphology (van Noordwijk *et al.*, 1980; Boag, 1983), behavior (Arnold, 1981a, b; Via, 1984a, b), physiology (Curtsinger and Laurie-Ahlberg, 1981), and other traits that are ecologically important and have a strong influence upon fitness. Current studies focus on understanding the role of development in genetic variation for these traits. It is important to determine whether quantitative genetic variation for a trait is stable throughout the development of an organism. If the heritability of a trait changes during ontogeny, then natural selection can only influence the trait during intervals of high heritability. Conversely, if natural selection only occurs during certain periods of development, then the trait will be more free to vary during other portions of ontogeny.

The mud crab *Eurypanopeus depressus* (Smith) has several features which will make it suitable for a quantitative analysis of growth and development. Like other arthropods, changes in size and shape in *Eurypanopeus* is restricted to a short interval following a molt while the new exoskeleton is still flexible. In addition, molting of the exoskeleton uniquely defines developmental events. In many nonarthropod species the accurate assessment of developmental progress or developmental staging is either difficult or is a largely arbitrary process. Accurate developmental assessment is essen-

Received 22 June 1987; accepted 26 August 1987.

[1] Contribution number 688 from the Belle W. Baruch Institute for Marine Biology and Coastal Research.

tial to an understanding of changes in heritability during ontogeny. Finally, in *Eurypanopeus*, early juvenile development includes a rapid change in shape. During the first three juvenile molts, these crabs transform from a megalops with a square carapace to the trapezoidal shape typical of the adult stage in this species. These characteristics allow us to address several fundamental questions on the quantitative genetics of juvenile growth and form. We will determine the relative importance of genetic causes to the variance in early juvenile growth and shape in *Eurypanopeus*. We will also determine whether genetic variation in these traits varies during development and whether the genetic component of variance changes during the transformation in shape that occurs early in juvenile development.

Materials and Methods

Eurypanopeus depressus is the most common mud crab inhabiting oyster reefs along the east coast of the United States (Williams, 1984) and is abundant in intertidal oyster reefs in South Carolina. Ovigerous females are found from April to November in the North Inlet estuary (Georgetown, South Carolina). Costlow and Bookhout (1961) described the larval development of this species reared under laboratory conditions. They reported four zoeal stages and a megalops.

Gravid *Eurypanopeus depressus* females were collected at the Baruch Institute Field Laboratory near Georgetown, South Carolina, during the summer of 1978. All females used in this study were collected at one time. Each female was maintained in the laboratory at 25°C and a 14:10 h light:dark cycle in an individual bowl of 30‰ seawater until an egg mass was expelled. Egg clutches from six females were hatched and individually reared in beakers through the zoeal stages. Zoeae were maintained under the same environmental conditions as their mothers and were fed freshly hatched *Artemia ad libitum*.

Upon metamorphosis to the megalops stage, juveniles crabs were transferred to individual cells in a compartmented box where they were maintained with seawater (30‰ and 25°C). To reduce the effects of a shared environment, the compartmentalized boxes were returned to the incubator in a random placement following a daily change in seawater. Juvenile crabs were fed excess amounts of freshly hatched *Artemia* daily. Individual crabs were checked daily for a molted exoskeleton. Upon molting the exoskeleton was removed and the crab was measured for both carapace length and width to the nearest 0.01 mm using an ocular micrometer on a dissecting microscope. Carapace length was measured as the distance between the anterior and posterior margins of the shell. Width was measured as the maximal distance across the lateral margins of the shell. The number of days elapsed since metamorphosis to megalops was recorded at each molting. During the experiment individual animals died, so sample sizes vary throughout the analysis. Measurements continued for eight successive molts but numbers declined significantly after the sixth molt. Therefore, the analysis reported here is restricted to the first six molts.

Genetic and statistical analysis

Data were collected such that members of the same family could be distinguished throughout the analysis. Quantitative genetics uses the similarity among relatives to determine the proportion of the phenotypic variance in a trait that can be explained by genetic variance (Falconer, 1981). Therefore, if the mean value for a trait, such as body size, varies significantly among families this implies that close relatives may

appear similar because of the genes they share in common. It is also possible that relatives are similar in appearance for non-genetic reasons. These possibilities are discussed below. In this analysis we know whether two individuals share the same mother; we do not know whether they share the same father. Therefore it is unknown whether offspring derived from the same clutch are full- or half-siblings. Without knowing the exact genetic relationship among siblings it is impossible to estimate heritability (genetic variance/total phenotypic variance) accurately. However, we can estimate whether there is a significant genetic effect upon the phenotypic variance observed in these samples of juvenile crabs. This analysis is similar to that used in other studies of quantitative genetics using wild-caught pregnant females (Arnold, 1981a, b).

Relative growth rates were determined by regressing the change in size between successive molts against initial size for each individual within a family. Variation among families in relative growth was then analyzed using analysis of covariance. Relative growth rates are reported as mm growth/mm initial size. Relative growth rates were determined for both length and width and were calculated on a per molt and per day basis (see below). Development rate was calculated as the number of days required to proceed from one molt to the next. Variation among families in development rate was analyzed using ANOVA. *Eurypanopeus depressus* varies dramatically in shape during juvenile development. Shape can be expressed as the ratio of width to length. However, ratios have unusual sampling distributions and ANOVA is not an appropriate methodology for their analysis (Atchley *et al.*, 1976). Therefore, carapace length was regressed against width for each family and analysis of covariance used to determine whether there was significant variation among families in either slopes or adjusted means of the regressions.

Relative growth rates are expressed in two ways. First, the relative growth between two successive molts was determined by regressing the change in size against initial size for each family. Variation among families was then analyzed using ANCOVA. The analysis of covariance reports the average change in size for each family adjusted to the average initial size for all families. Relative growth rates were then calculated by dividing each adjusted mean by the average initial size. Therefore, relative growth rates are reported as mm growth/mm initial size/molt (mm/mm/molt). This method of expressing relative growth indicates the change in size between molts but does not account for the amount of time required to proceed from one molt to the next. Therefore growth rates were also calculated by determining the change in size between successive molts for each individual and dividing by the intermolt interval for that individual. This quantity was then regressed against initial size to determine relative growth rates and the data analyzed by ANCOVA.

The family means for all growth and development rate measurements are presented in graphical form. It was not possible to simultaneously present the standard errors of the means for these analyses without obscuring the graphical presentations. Therefore the following convention was adopted to provide a representation of the variance about each family mean. The error mean square is reported for each analysis of variance in tabular form. Combined with the sample sizes for each family these data may be used to calculate either standard errors or confidence limits for the family means (Sokal and Rohlf, 1981). The six families used in this study varied in size. In addition, some individuals died and occasionally individual measurements were lost. Therefore sample sizes within a family vary slightly from one experiment to the next. Average sample size and the range in sample size for each family are: family 1, 10.2

TABLE I

F-tests of variation among families in growth and development rates. Error mean squares are also reported for each test

	Molt interval				
	1–2	2–3	3–4	4–5	5–6
GROWTH RATE					
Length/Molt					
F-value	3.61 (102)**	3.29 (110)**	1.98 (112)	2.14 (107)	1.83 (84)
error MS	0.0098	0.0085	0.0170	0.0079	0.0058
Width/Molt					
F-value	3.21 (112)**	1.65 (117)	6.20 (115)***	0.23 (112)	1.65 (89)
error MS	0.0137	0.0100	0.0075	0.0041	0.0044
Length/Day					
F-value	4.00 (94)***	0.54 (112)	0.92 (112)	2.64 (107)*	4.09 (78)**
error MS	0.00105	0.00105	0.00047	0.00023	0.00005
Width/Day					
F-value	4.75 (102)***	0.74 (117)	4.56 (115)***	1.62 (112)	3.33 (88)*
error MS	0.00105	0.00104	0.00023	0.00018	0.00009
DEVELOPMENT RATE					
F-value	4.10 (110)***	1.25 (120)	3.29 (119)**	2.70 (115)*	6.04 (94)***
error MS	5.99	2.02	4.29	24.95	17.53

The denominator degrees of freedom are reported in parenthesis. The numerator degrees of freedom are equal to 5 in all cases. The significance of the F-test is indicated by an asterisk (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$). F-values without an asterisk are not significant at the 5% level.

(7–12); family 2, 13.5 (11–15); family 3, 17.1 (10–20); family 4, 21.7 (18–24); family 5, 38.6 (31–42); and family 6, 12.1 (11–13).

RESULTS

Relative growth per molt

Relative increases in length varied with development and among families. Between the first and second molt the average relative growth rate was 0.25 mm/mm/molt and there was significant variation among families in their average growth rate ($P < 0.01$, Table I). Families 1, 3, 5, and 6 exhibited high growth rates of approximately 0.25 mm/mm/molt while families 2 and 4 exhibited much lower growth rates of approximately 0.17 mm/mm/molt (Fig. 1). The error mean square for relative growth rates over this first interval and all subsequent analyses are presented in Table I.

Between the second and third molt families 1, 3, 5, and 6 continued to grow at significantly higher rates than did families 2 and 4 ($P < 0.01$, Table I). The highest relative growth rates were observed between the third and fourth molt, averaging 0.36 mm/mm/molt (Fig. 1). However the variation among families was not significant during this interval. Average growth rates dropped to 0.16 mm/mm/molt in the next two molt intervals (molt 4–5 and 5–6), and there was no significant variation among families (Fig. 1; Table I). In summary, there was significant variation among families in relative growth rate for length in the first two molt intervals. There was no signifi-

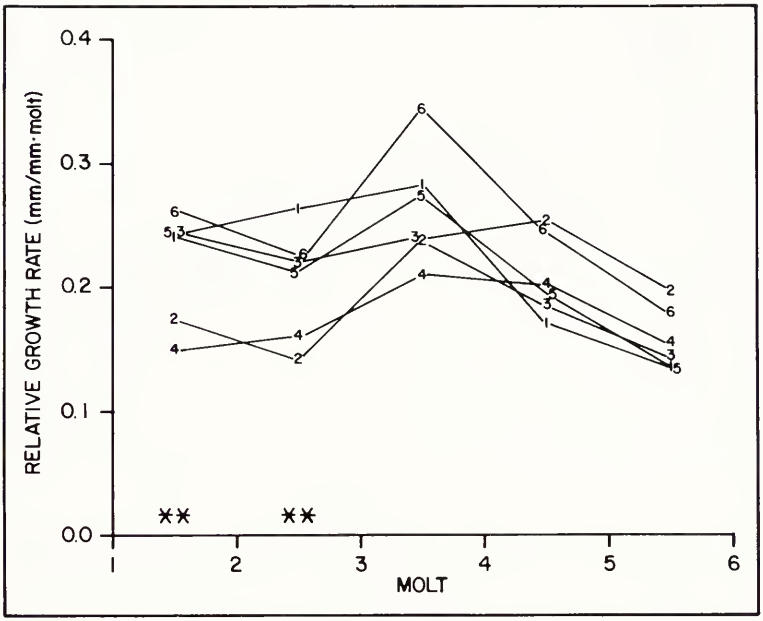

FIGURE 1. Relative growth rates in length for *Eurypanopeus depressus* for each intermolt interval. Growth rates are reported in mm/mm/molt. Each symbol indicates the mean growth rate for each of the six families used in the analysis. Significant variation among families is indicated along the abcissa with an asterisk (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$).

cant variation among families in relative growth rate as development progressed beyond the third molt.

Similar to growth in length, relative changes in width depended on both development and family. Relative growth rates were initially high, averaging 0.30 mm/mm/molt between molts 1 and 2. Between molts 5 and 6 these rates declined to an average value of 0.17 mm/mm/molt (Fig. 2). There was significant variation among families in relative growth rate between molts 1 and 2 ($P < 0.01$, Table I) and molts 3 and 4 ($P < 0.001$, Table I). Family 6 was the fastest growing group in virtually all molt intervals. Families 2 and 4 were initially the slowest growing families, but by the final molt interval they were among the most rapidly growing families. This change in relative growth rates was similar to that observed for growth in length. Variation in relative growth in width was not significant among families in any other molt interval (Fig. 2; Table I).

Relative daily growth

Relative growth rates were also calculated by dividing the change in size between molts by the interval between molts. This method of expressing relative growth provides a daily estimate of growth but also includes two potentially genetically variable parameters; growth and development time. An alternate way of viewing this expression of growth is that it removes a potential artifact in the previous expression by controlling for variation in intermolt intervals. In many species growth between molts

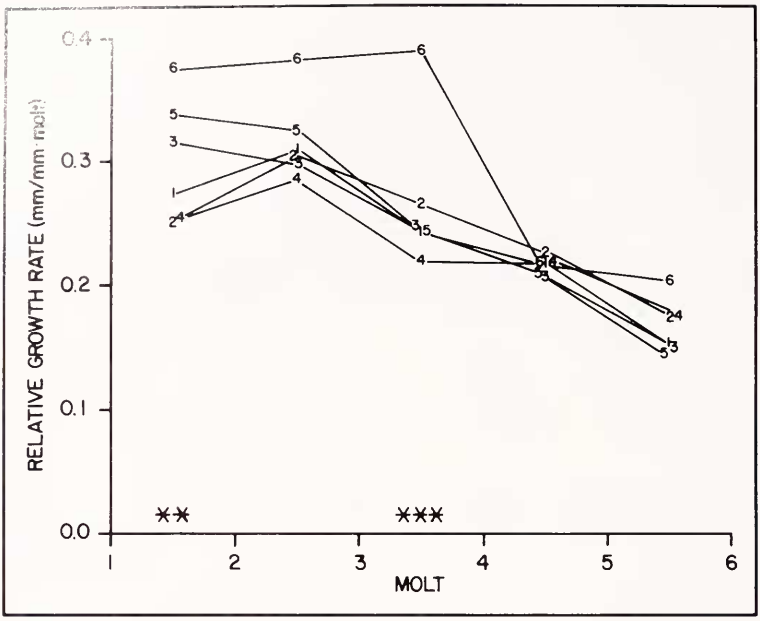

FIGURE 2. Relative growth rates in width for *Eurypanopeus depressus* for each intermolt interval. Growth rates are reported in mm/mm/molt. Each symbol indicates the mean growth rate for each of the six families used in the analysis. Significant variation among families is indicated along the abcissa with an asterisk (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$).

is a function of the length of time between molts. Therefore the previous analysis may confuse variation in the interval between molts with variation in growth rate. This artifact is minimized by expressing relative growth on a daily rather than per molt basis.

Relative daily growth in length varied during development and was strongly dependent upon family. Relative increase in length was initially high, averaging 0.049 mm/mm/day, but declined steadily with each molt (Fig. 3). The average daily growth rate was 0.015 mm/mm/day between the fifth and sixth molts. Daily growth rates in length also exhibited a significant family effect. Between molts 1 and 2, families 1, 3, 5, and 6 grew at nearly double the rates of families 2 and 4 ($P < 0.001$; Table I; Fig. 3). In the interval between molts 2 and 3 and between molts 3 and 4 there were no significant differences among families in daily growth rates (Table I). The variance in daily growth rate among families was again significant ($P < 0.05$; Table I) between molts 4 and 5. There was also significant variation among families between molts 5 and 6 ($P < 0.01$, Table I). There was a clear change in the rank order of relative growth rates among the families with progressing development. Families 2 and 4 were initially the slowest growing groups, but by the final molt interval they were the fastest growing families (Fig. 3).

Relative daily growth rates for width decreased steadily with each successive molt. Initially relative growth rates in width were 0.067 mm/mm/day and declined to 0.016 mm/mm/day by the final molt interval (Fig. 4). As with previous measures of growth, relative daily growth in width also depended upon family. Between molts 1 and 2, the variation among families was highly significant ($P < 0.001$, Table I). Between

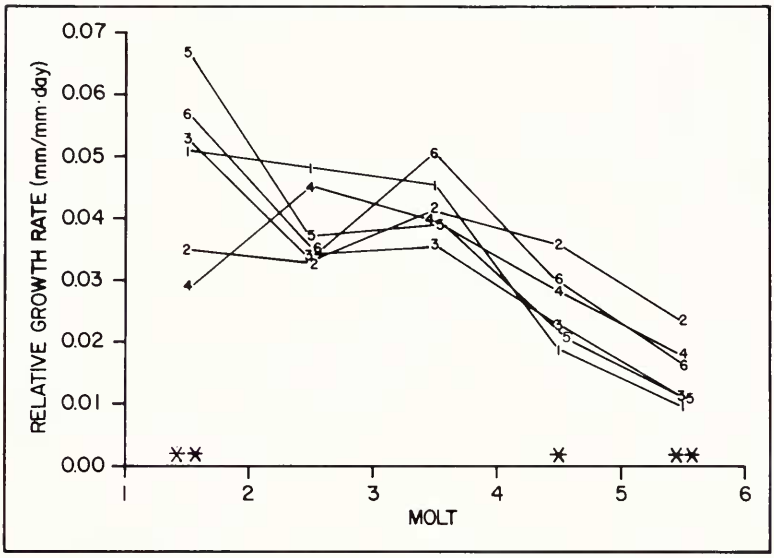

FIGURE 3. Relative daily growth rates in length for *Eurypanopeus depressus* for each intermolt interval. Growth rates are reported in mm/mm/day. Each symbol indicates the mean growth rate for each of the six families used in the analysis. Significant variation among families is indicated along the abcissa with an asterisk (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$).

molts 2 and 3 there was no significant variation among families in relative daily growth. Between molts 3 and 4 there was again significant variation among families ($P < 0.001$, Table I). Between molts 4 and 5 there was no significant variance among families while in the final molt interval the variation among family means was significant ($P < 0.05$, Table I). As with previous analyses, families 2 and 4 initially exhibited low relative growth rates and ultimately became the fastest growing families by the final molt (Fig. 4).

Development rate

The intermolt interval increased with development. The interval between the first and second molt averaged 5.2 days while it required about 12.8 days to proceed from molt 5 to 6 (Fig. 5). The variation among families changed substantially over the course of development. Early in development, between molts 1 and 2, variation among families was highly significant ($P < 0.001$, Table I). This variation was due primarily to the relatively long intermolt period of families 3 and 4 (Fig. 5). The time required to proceed from molt 2 to 3 was virtually identical in all cases; the variation among families was not significant. After the third molt, families 2 and 4 exhibited a large decrease in the intermolt interval relative to the other families. By the final molt interval these two families had an intermolt period 35% lower than the other four families (Fig. 5). The variation among families in intermolt time was also significant for the intervals between molts 3 and 4, molts 4 and 5, and molts 5 and 6 (Table I).

Shape

Carapace width initially increased at much higher rates than did length. Ultimately the rates of increase in width and length converged by the final molt interval.

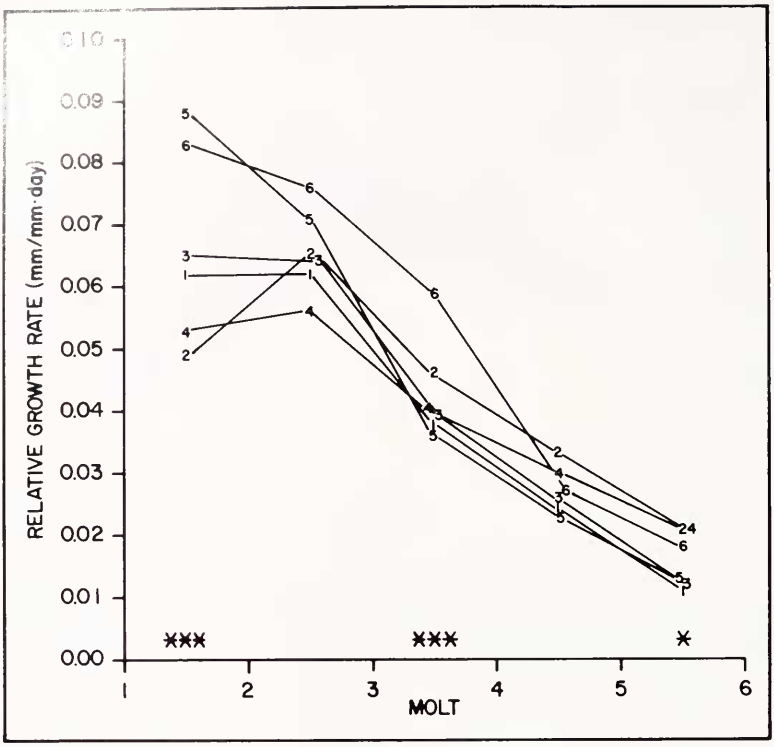

FIGURE 4. Relative daily growth rates in width for *Eurypanopeus depressus* for each intermolt interval. Growth rates are reported in mm/mm/day. Each symbol indicates the mean growth rate for each of the six families used in the analysis. Significant variation among families is indicated along the abcissa with an asterisk ($*P < 0.05$, $**P < 0.01$, $***P < 0.001$).

This resulted in a major change in shape over the first few juvenile molts. After metamorphosis to the first crab stage the carapace of *Eurypanopeus depressus* is approximately square, with an average width to length ratio of 0.98 (Fig. 6). During the second molt the ratio of width to length increased to 1.08. The ratio increased to 1.2 during the third molt. During molts 4, 5, and 6 there was a gradual but continual increase in the width to length ratio up to an average of 1.24 (Fig. 6). By the sixth molt the crabs had adopted the trapezoidal shape characteristic of adult *Eurypanopeus*.

The analysis of shape was designed to test two questions: do families vary in shape and where in ontogeny is this source of variance of greatest importance? Carpace width was regressed against length for each family, and ANCOVA was used to determine if there was significant variation in shape among families at each molt. Significant variation in adjusted means indicates that some families are consistently broader or narrower than others. Significant variation among slopes of these regressions indicates that the manner in which width scales onto length depends upon family. Therefore, either variation in adjusted means or slopes would be indicative of shape variation among families.

Variation in adjusted means was not significant for any of the six molts (Fig. 6; Table II). With the exception of the sixth molt there were also no significant differ-

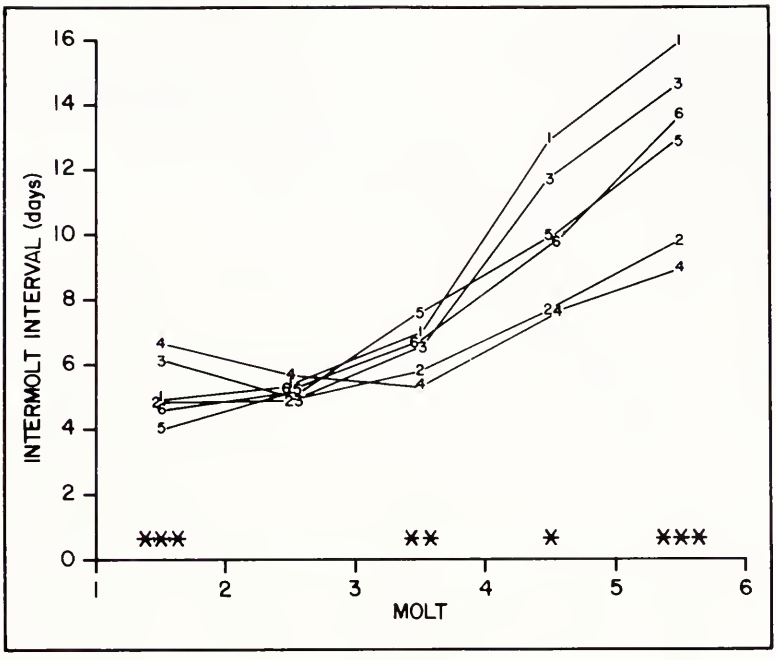

FIGURE 5. Mean development rates for six families of *Eurypanopeus depressus* for each intermolt interval. Development rates are reported as the days required to proceed from one molt to the next. Significant variation among families is indicated along the abcissa with an asterisk (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$).

ences among families in the slope of the width on length regressions (Table II). In the sixth molt there was significant variation among families in the slopes of these regressions ($0.01 < P < 0.05$). However this one case of significance may be due to random chance. There were 12 tests of significance performed in this analysis, of which one was significant at the 0.05 level. Rejections at this significance level should occur by chance 5% of the time (0.6 times in 12 tests). It should also be noted from Figures 1 and 2 that there was no significant variation among families in increases in either width or length which also suggests that the significance of variation in shape among families during this interval was spurious. In summary, there is no convincing evidence of significant variation in shape among the six families used in this analysis.

DISCUSSION

There was significant variation among families in relative growth rates. This was true for rates of increase in both width and length and for growth rates calculated on both a per molt and daily basis. Variation in growth rate was observed throughout juvenile development; every molt interval included significant family variation in at least one of the measures of relative growth rate. Natural selection must operate on traits that retain significant genetic variation and there has been considerable interest in the manner in which heritable variation may be distributed through development. For *Eurypanopeus depressus*, genetic variation for growth rate persists for all juvenile

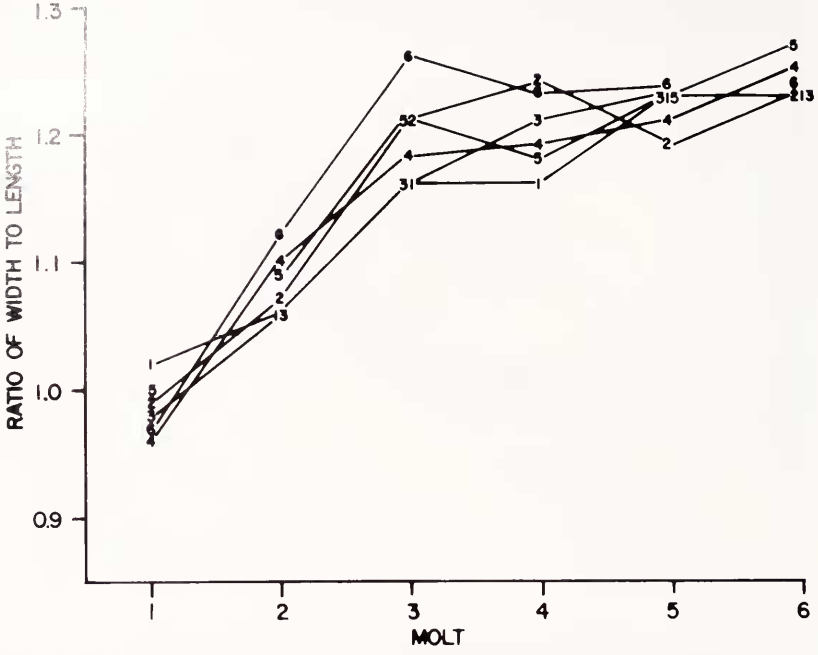

FIGURE 6. Width to length ratios for six families of *Eurypanopeus depressus* after the first six juvenile molts. Width to length ratios are mean values for each family.

developmental stages. Therefore, natural selection could potentially affect growth rate in this species at any point during its juvenile development.

The development rate also varied among families. This variation must explain in part the growth rate variation observed among families. In general, high growth rates in any given interval were inversely correlated with the duration of an intermolt interval. Rapid growth and rapid development appear to co-occur during development. However, this correlation has little bearing on the variation in growth observed

TABLE II

Results of ANCOVA of carapace width regressed against length for each family at each molt

Molt	F (adjusted means)	F (slopes)
1	1.57 (121)	1.85 (116)
2	1.32 (119)	0.76 (114)
3	1.40 (118)	1.80 (113)
4	1.26 (118)	0.53 (113)
5	0.85 (114)	1.05 (109)
6	0.89 (90)	2.59* (85)

F values for tests of homogeneity of adjusted means and slopes are given. The numerator degree of freedom was 5 in every test. The denominator degrees of freedom are given in parenthesis.

* $P < 0.05$.

among families. We correlated the growth and development rates of each family within a molt interval; there were no significant correlations between growth and development rates within any molt interval. This lack of correlation is exemplified by the interval between the second and third molt in which intermolt intervals were identical for all six families yet there was considerable variation in growth. In addition, one would expect that expressing growth rate on a daily basis would reduce any role of development rate in indirectly explaining among family variation in growth. This was clearly not the case—the expression of growth on a daily basis appeared to increase the differences among families. Therefore, it appears that families of *Eurypanopeus depressus* differ in both growth and development rates and that these interact in a complex manner.

While it is apparent that there is substantial variation among families in rates of growth and development, the origin of this variation is not obvious. Significant covariation among family members may be due to genetic causes or to a shared environment (Falconer, 1981). The most obvious source of a common environment that may lead to covariation among siblings is a maternal effect. However it is also possible that a shared environment during the larval culture phase could lead to significant elevation in the similarity among relatives. With the experimental design used here it is not possible to unequivocally reject the hypothesis of maternal effects leading to the observed variation among families. However, the pattern of growth rate variation among families indicates that maternal effects are an unlikely explanation for these results. One consistent trend in the growth data was that families 2 and 4 initially exhibited low growth rates which increased during development until in most cases they became the most rapidly growing families. The other four families were typically fast growing during the initial molts and then declined in their relative growth rates. Maternal effects might have a reasonably consistent impact on the growth of each family. For example, if a female produces high quality eggs, perhaps by the inclusion of atypically high yolk levels, the offspring born to that female should consistently grow faster than offspring produced from inferior eggs. What was observed here was a relative growth advantage of some families that changes during ontogeny. This switching of growth advantage is difficult to explain by maternal or other common environmental effects. Therefore we conclude that a significant proportion of the variation in growth and development observed among families is of genetic origin.

In a conventional quantitative genetic design, controlled matings are produced in which paternal effects can be quantified and the degree of genetic relation among offspring known. The study of genetic variation in natural populations has certain liabilities that are exemplified in this study. The first has been discussed. By using wild-caught ovigerous females the among family variation includes both genetic and maternal effects. This design is similar to that of Arnold (1981a, b) who used pregnant female garter snakes to generate families of full-siblings.

A second problem with using wild-caught pregnant females is that we are uncertain as to the genetic relationship among siblings. Individuals born to a given female may be either full- or half-siblings depending upon the mating system of the population under investigation. Many species of brachyuran crabs store sperm from multiple matings (Sastry, 1983). Therefore the offspring of a single *Eurypanopeus* female are likely to be a combination of full and half-siblings. Without knowing the exact genetic relationship among offspring, it is impossible to partition the variance in a trait into genetic and environmental sources or to subpartition the genetic variance into additive and nonadditive components. While we cannot accurately estimate the magnitude of the genetic contribution to the variation in growth and development

rates, it is clear that a substantial fraction of this variation must be genetic in origin. Family effects were very striking; in many incidences family explained greater than 20% of the total variation observed in relative growth rates. Therefore genetic variation for growth in *Eurypanopeus depressus* is prevalent but a more controlled breeding design would be required to produce an accurate estimate of its magnitude.

Genetic variation in growth has been observed in other marine invertebrates. Single or multilocus genetical analysis of enzyme-coding genes has often revealed a significant genetic component to growth (Zouros *et al.,* 1980; Garton, 1984; Koehn and Gaffney, 1984). Quantitative genetic analysis also revealed that a substantial fraction of the observed variation in growth in marine bivalves is of genetic origin (Lannan, 1972; Newkirk *et al.,* 1977, 1981). This study likewise found a large proportion of the variation in growth is due to genetic variation.

There was no evidence that shape of the carapace in *Eurypanopeus depressus* was genetically variable. This was surprising in light of the highly significant variation among families in increase in both width and length which are the two parameters used to determine carapace shape. There is increasing interest in the analysis of shape and in the role ontogeny plays in altering genetic variances in morphology (Atchley and Rutledge, 1980; Leamy and Cheverund, 1984). Recently, Riska *et al.* (1984) demonstrated that morphological traits may have high levels of quantitative genetic variation associated with them early in juvenile development, but following the attainment of adult stature this genetic variation is sharply reduced. This study on mice illustrates the commanding role ontogeny may have in the expression of genetic variation. In the present study, we expected to observe significant family effects on shape, particularly between the second and third molt when shape changed rapidly. This was not the case. There was only one incidence of significant variation among families in shape and this case was probably not meaningful. Therefore we conclude that in *Eurypanopeus depressus* growth and development rates are genetically variable while shape is a highly conserved trait, exhibiting virtually no genetic variation during juvenile development.

ACKNOWLEDGMENTS

We thank Dr. David Lincoln for critically reading an earlier draft of this paper.

LITERATURE CITED

ARNOLD, S. J. 1981a. Behavioral variation in natural populations. I. Phenotypic, genetic and environmental correlations between chemoreceptive responses to prey in the garter snake, *Thamnophis elegans. Evolution* **35:** 489–509.

ARNOLD, S. J. 1981b. Behavioral variation in natural populations. II. The inheritance of feeding response in crosses between geographic races of the garter snake, *Thamnophis elegans. Evolution* **35:** 510–515.

ATCHLEY, W. R., C. T. GASKINS, AND D. ANDERSON. 1976. Statistical properties of ratios. I. Empirical results. *Syst. Zool.* **25:** 137–148.

ATCHLEY, W. R., AND J. J. RUTLEDGE. 1980. Genetic components of size and shape. I. Dynamics of components of phenotypic variability and covariability during ontogeny in the laboratory rate. *Evolution* **34:** 1161–1173.

BOAG, P. T. 1983. The heritability of external morphology in Darwin's ground finches (*Geospiza*) on Isla Daphne Major, Galapagos. *Evolution* **37:** 877–894.

COSTLOW, J. D., AND C. G. BOOKHOUT. 1961. The larval development of *Eurypanopeus depressus* (Smith) under laboratory conditions. *Crustaceana* **2:** 6–15.

CURTSINGER, J. W., AND C. C. LAURIE-AHLBERG. 1981. Genetic variability of flight metabolism in *Drosophila melanogaster* I. Characterization of power output during tethered flight. *Genetics* **98:** 549–564.

FALCONER, D. S. 1981. *Introduction to Quantitative Genetics.* Longman Inc., New York. 340 pp.

GARTON, D. W. 1984. Relationship between multiple locus heterozygosity and physiological energetics of growth in the estuarine gastropod *Thais haemastoma. Physiol. Zool.* **57:** 530–543.

KOEHN, R. K., AND P. M. GAFFNEY. 1984. Genetic heterozygosity and growth rate in *Mytilus edulis. Mar. Biol.* **82:** 1–8.

LANNAN, J. E. 1972. Estimating heritability and predicting response to selection for the Pacific oyster, *Crassostrea gigas. Proc. Natl. Shellfish Assoc.* **62:** 62–66.

LEAMY, L., AND J. M. CHEVERUND. 1984. Quantitative genetics and the evolution of ontogeny. II. Genetic and environmental correlations among age-specific characters in randombred mice. *Growth* **48:** 339–353.

NEWKIRK, G. F., L. E. HALEY, D. L. WAUGH, AND R. W. DOYLE. 1977. Genetics of larvae and spat growth in the oyster, *Crassostrea virginica. Mar. Biol.* **41:** 49–52.

NEWKIRK, G. F., L. E. HALEY, AND J. DINGLE. 1981. Genetics of the blue mussel *Mytilus edulis* (L): nonadditive genetic variation in larval growth rate. *Can. J. Genet. Cytol.* **23:** 349–354.

VAN NOORDWIJK, A. J., J. H. VAN BALEN, AND W. SHARLOO. 1980. Heritability of ecologically important traits in the great tit, *Parus major. Ardea* **68:** 193–203.

RISKA, B., W. R. ATCHLEY, AND J. J. RUTLEDGE. 1984. A genetic analysis of targeted growth in mice. *Genetics* **107:** 79–101.

SASTRY, A. N. 1983. Ecological aspects of reproduction. Vol. 8. Pp. 179–270 in *Biology of Crustacea,* F. J. Vernberg and W. B. Vernberg, eds. Academic Press, New York.

SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry.* W. H. Freeman and Co., San Francisco. 859 pp.

VIA, S. 1984a. The quantitative genetics of polyphagy in an insect herbivore. I. Genotype-environment interactions in larval performance on different host plant species. *Evolution* **38:** 881–895.

VIA, S. 1984a. The quantitative genetics of polyphagy in an insect herbivore. II. Genetic correlations in larval performance within and among host plants. *Evolution* **38:** 896–995.

WILLIAMS, A. B. 1984. *Shrimps, Lobsters, and Crabs of the Atlantic Coast of the Eastern United States, Maine to Florida.* Smithsonian Institution Press, Washington, DC. 550 pp.

ZOUROS, E., S. M. SINGH, AND H. E. MILES. 1980. Growth rate in oysters: an overdominant phenotype and its possible explanations. *Evolution* **34:** 856–867.